



Generic Limits of *Dryopetalon*, *Rollinsia*, *Sibara*,
and *Thelypodiopsis* (Brassicaceae), and a Synopsis of *Dryopetalon*

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ABSTRACT. The genus *Rollinsia* Al-Shehbaz is reduced to synonymy of *Dryopetalon* A. Gray (Brassicaceae), and the characters distinguishing the latter from *Sibara* Greene and *Thelypodiopsis* Rydberg are discussed. An expanded description of *Dryopetalon* (southern United States and northern Mexico) and a key, synonymies, and distributions of its eight species are presented. The new combinations *D. breedlovei* (Rollins) Al-Shehbaz, *D. byei* (Rollins) Al-Shehbaz, *D. paysonii* (Rollins) Al-Shehbaz, and *D. viereckii* (O. E. Schulz) Al-Shehbaz are proposed. *Dryopetalon purpureum* Rollins is reduced to synonymy of *D. palmeri* (S. Watson) O. E. Schulz, and *D. crenatum* var. *racemosum* Rollins and *D. runcinatum* var. *laxiflorum* Rollins are reduced to synonymy of their respective species. *Arabis endlichii* O. E. Schulz is lectotypified.

Key words: Brassicaceae, *Dryopetalon*, Mexico, *Rollinsia*, *Sibara*, *Thelypodiopsis*, United States.

During work on the treatment of Brassicaceae for an upcoming volume of the *Flora of North America* (FNA), the morphological boundaries of several genera are critically evaluated, especially in light of available molecular data (e.g., Warwick et al., 2002, 2006) and the most recent tribal classification of the family (Al-Shehbaz et al., 2006). This action required the examination of all species of *Dryopetalon* A. Gray, *Rollinsia* Al-Shehbaz, *Sibara* Greene, and *Thelypodiopsis* Rydberg, including several that occur south of the FNA area in Mexico. The present paper focuses on the species included herein in *Dryopetalon*.

DRYOPETALON

The North American *Dryopetalon* was established by Gray (1853) as a monotypic genus readily distinguished from the other genera of Brassicaceae (Cruciferae) by having lobed petals superficially resembling the leaves of certain oaks. Schulz (1929) added another species originally described as *Cardamine plameri* S. Watson, and the genus remained ditypic in Schulz's (1936) comprehensive monograph of the family. Rollins (1941, 1984) added three species, and as it stands now (Rollins, 1993; Appel & Al-Shehbaz, 2003), *Dryopetalon* consists of five species and three varieties.

Schulz (1936) placed *Dryopetalon*, along with the Chilean-Argentinean *Schizopetalon* Sims (10 species; Al-Shehbaz, 1989) and the Mexican *Ornithocarpa* Rose (two species; Rollins, 1969), in the Schizopetaleae, a tribe he delimited solely on the basis of having lobed or fimbriate petals. In their recent tribal classification of the family, Al-Shehbaz et al. (2006) placed *Ornithocarpa* in the tribe Cardamineae, maintained both *Dryopetalon* and *Schizopetalon* in the Schizopetaleae, and expanded the latter tribe to include at least 20 genera, of which 18 have entire petals.

As delimited by Rollins (1993), *Dryopetalon* shows tremendous variation in the development of the petal lateral teeth or lobes. For example, in *D. runcinatum* A. Gray, the generic type, the petals are 2- to 5-toothed or -lobed on each side, whereas in *D. palmeri* (S. Watson) O. E. Schulz they show continuous variation from being obscurely crenate to strongly laciniate at the margin, and in *D. membranifolium*

Rollins the petals are deeply emarginate at the apex and have no lateral lobes.

Studies on *Arabidopsis thaliana* (L.) Heynhold show that the loss of function in the JAGGED gene or in the sterol biosynthesis gene *FRL1* leads to the formation of toothed or serrated petals (Dinneen et al., 2004; Hase et al., 2005). These findings imply that the development of toothed petals can be controlled by simple Mendelian inheritance. It is not known if a similar genetic basis exists in *Dryopetalon*, but these mutations in *A. thaliana* should warn against the overemphasis of characters such as petal margin as the main criterion to delimit genera at the expense of the overall morphology. Several genera of the Brassicaceae encompass variation in petal morphology comparable to that of *Dryopetalon*. For example, *Draba* L. includes species with deeply 2-lobed and entire petals, whereas the Himalayan *Megacarpaea* DC. has eight species with entire petals and only one, *M. delarayi* Franchet (China), has entire or shallowly to deeply 3(or 5)-lobed petals (Zhou et al., 2001). Evidently, lobed petals evolved independently multiple times within the Brassicaceae. In delimiting *Dryopetalon*, I depend on all features of the plant and put less emphasis on the petal margin. In so doing, some of the species recognized herein have entire petals.

THELYPODIOPSIS

Schulz (1936) placed *Thelypodiopsis* (western United States, northern Mexico) in the tribe Hesperiideae and *Dryopetalon* in the Schizopetaleae, whereas Al-Shehbaz et al. (2006) place both genera in the latter tribe. Indeed, the similarities between some species currently assigned to the two genera are so substantial that there is some justification to Rollins' (1984: 22) statement: "There is such a close resemblance between *D. membranifolium* and those of *Thelypodiopsis* *byei* and *T. breedlovei*, both of which have entire petals, that it is among these species where *Thelypodiopsis* and *Dryopetalon*, as genera, come close together." In the absence of flowering material, Rollins (1982b) indicated that it is almost impossible to reliably assign specimens of the above three species to genera. However, despite the overwhelming similarities in all other characters, he depended solely on the petal margin and apex in the generic disposition of these species.

Rollins (1976, 1982b, 1984) gradually expanded the limits of *Thelypodiopsis* well beyond the original delimitation proposed by Rydberg (1907) and later refined by Al-Shehbaz (1973). Of the 17 species recognized by Rollins (1993) in *Thelypodiopsis*, only seven (*T. ambigua* (S. Watson) Al-Shehbaz, *T. aurea* (Eastwood) Rydberg, *T. divaricata* (Rollins) S. L. Welsh & Reveal, *T. elegans*

(M. E. Jones) Rydberg, *T. juniperorum* (Payson) Rydberg, *T. vermicularis* (S. L. Welsh & Reveal) Rollins, and *T. wootonii* (B. L. Robinson) Rollins) are retained by the present author in this genus. Both *T. breedlovei* Rollins and *T. byei* Rollins are transferred herein to *Dryopetalon*, whereas *T. alpina* (Standley & Steyermark) Rollins is retained in *Romanschulzia* O. E. Schulz, and the remaining seven species are being studied for placement in a fourth genus.

As delimited by Al-Shehbaz (1973), *Thelypodiopsis* includes species with prominently 2-lobed stigmas, linear anthers 2.5–4 mm long, distinct gynophores up to 9 mm long, and oblanceolate petal claws well differentiated from the blade. Both *T. breedlovei* and *T. byei*, as well as all *Dryopetalon*, have subentire or only obscurely lobed stigmas, ovate to oblong anthers rarely exceeding 1 mm in length, often obsolete gynophore, and petals often undifferentiated into blade and claw or gradually attenuated into a claw-like base.

ROLLINSIA

Rollinsia was recognized by Al-Shehbaz (1982) as a monotypic genus based on a species originally described by Rollins (1957) as *Thelypodium paysonii* Rollins. The characters used to distinguish *Rollinsia* from *Thelypodium* Endlicher are the presence in *Rollinsia* of pubescent (vs. glabrous) bases of filaments and petal claws, non-torulose (vs. torulose) fruits, and a chromosome number of $2n = 20$ (vs. $2n = 26$). All of the above features of *Rollinsia* are present in *Dryopetalon*, especially *D. crenatum* (Brandegee) Rollins and *D. runcinatum*, both of which also have pubescent filament and petal bases, and *D. palmeri*, which has non-torulose fruits and slender gynophores. The original illustration of *T. paysonii* (Rollins, 1957: 63; duplicated in Rollins, 1993: 723) correctly shows the petals to have undulate or few-toothed margins, but this aspect of the species was overlooked. Indeed, in the absence of petals, it is virtually impossible to distinguish *T. paysonii* from species of *Dryopetalon*. Only *D. runcinatum* is known cytologically, and its $2n = 24$ (Warwick & Al-Shehbaz, 2006) represents a higher aneuploid number than that of *T. paysonii*. The latter species is transferred herein to *Dryopetalon*, and *Rollinsia* is consequently reduced to synonymy.

SIBARA

Although one of the six species initially assigned by Greene (1896) in *Sibara* is *Dryopetalon palmeri*, the remaining five species were maintained in *Sibara* by Schulz (1936), and the genus was expanded by Rollins (1947, 1982a) to include 10 species.

As later circumscribed by Rollins (1993), *Sibara* (southern United States, northern Mexico) represents a heterogeneous assemblage of 10 species currently assigned to four genera of two tribes. *Sibara virginica* (L.) Rollins is now recognized in *Planodes* Greene, a genus placed by Schulz (1936) in the tribe Arabideae and by Al-Shehbaz et al. (2006) in the tribe Cardamineae. Of the remaining nine species that belong to the Schizopetaleae, six are maintained by the present author in *Sibara*: *S. angelorum* (S. Watson) Greene, *S. brandegeana* (Rose) Greene, *S. deserti* (M. E. Jones) Rollins, *S. filifolia* (Greene) Greene, *S. laxa* (S. Watson) Greene, and *S. mexicana* (S. Watson) Rollins. One species, *S. grisea* Rollins, is a synonym of *Thelypodium texanum* (Cory) Rollins and will be treated as such for the FNA. Of the remaining two species, I have not seen any material of *S. mexicana*, a species known only from the type specimen. However, I have examined numerous collections of *S. niereckii* (O. E. Schulz) Rollins, and this species is transferred herein to *Dryopetalon*. *Sibara* is readily distinguished from the other North American genera of Brassicaceae by having very lax flowering racemes and pectinate or deeply pinnatisect leaves with siliform to narrowly linear lobes. *Dryopetalon* has dense, corymbose, flowering racemes and entire or runcinate to pinnatifid lower leaves with broad lobes. Almost all species of *Dryopetalon* are long-pilose or hirsute at the base of the stem, and the plants are never glaucous. By contrast, species of *Sibara* are glaucous and either glabrous throughout or puberulent with minute simple or forked trichomes.

An expanded description of *Dryopetalon*, as well as a key, enumeration, synonymies, and distributions of its species are provided below.

KEY TO THE SPECIES OF *DRYOPETALON*

- 1a. Cauline leaves sessile, auriculate to amplexicaul; fruit 2–3 mm wide; seeds 10 to 28 per fruit, winged . . . *D. viereckii*
- 1b. Cauline leaves petiolate, not auriculate; fruit 0.5–1.5(–2) mm wide; seeds 30 to 110 per fruit, wingless.
- 2a. Plants with flowers.
 - 3a. Petal margin pinnatifid, laciniate, or distinctly dentate.
 - 4a. Bases of petal claws and filaments glabrous; flowers purple. *D. palmeri*
 - 4b. Bases of petal claws and filaments pubescent or distinctly papillate; flowers white.
 - 5a. Leaves entire or shallowly dentate to crenate; petals 4.5–6 mm long *D. crenatum*
 - 5b. Leaves pinnatifid to runcinate; petals 6–12 mm long.
 - 3b. Petal margin entire or repand, rarely with a few obscure teeth.
 - 6a. Bases of petal claws and filaments pubescent *D. paysonii*
 - 6b. Bases of petal claws and filaments glabrous.
 - 7a. Petal apex deeply emarginate; cauline leaves entire or dentate *D. membranifolium*
 - 7b. Petals apex obtuse; at least some cauline leaves pinnately lobed.
 - 8a. Petals 5–6.5 × 2–2.5 mm, white; ovaries and young fruits stipitate. *D. breedlovei*
 - 8b. Petals 7–10 × 4–5.5 mm, lavender; ovaries and young fruits sessile *D. byei*
 - 2b. Plants with mature fruits.
 - 9a. Cauline leaves entire, rarely shallowly dentate or crenate.
 - 10a. Fruits 1.1–1.5 mm wide; fruiting pedicels 5–11(–13) mm long; style 1.5–2.5 mm long; petals if present dentate, obtuse at apex *D. crenatum*
 - 10b. Fruits 0.7–0.9 mm wide; fruiting pedicels 14–20 mm long; style to 1 mm long; petals if present entire, emarginate at apex. *D. membranifolium*
 - 9b. At least some cauline leaves pinnately lobed.
 - 11a. Fruits sessile or rarely subsessile and with a gynophore 0.1–0.4 mm long.

- 12a. Style 1.5–2.5 mm long; cotyledons incumbent; petals if present entire *D. byei*
 12b. Style 0.1–0.7(–1) mm long; cotyledons accumbent; petals if present pinnatifid *D. runcinatum*
 11b. Fruits on a distinct gynophore (0.6)1–3 mm long.
 13a. Fruits 0.5–0.8 mm wide; seeds 0.6–0.9 × 0.5–0.6 mm; stigma slightly 2-lobed *D. breedlovei*
 13b. Fruits 1.3–2 mm wide; seeds 1–1.7 × ca. 1 mm; stigma entire.
 14a. Style cylindrical; gynophore 0.6–1 mm long; uppermost leaves coarsely dentate; petals
 if present purple, dentate to laciniate *D. palmeri*
 14b. Style often conical; gynophore 1–3 mm long; all leaves pinnatifid; petals if present
 white, entire *D. paysonii*

1. *Dryopetalon breedlovei* (Rollins) Al-Shehbaz, comb. nov. Basionym: *Thelypodiopsis breedlovei* Rollins, Contr. Gray Herb. 214: 26. 1984. TYPE: Mexico. Sinaloa: Mun. Sinaloa, Sierra Surutato, Cañon de Tarahumares betw. Arroyo Verde & Rancho Tarahumares, steep N-facing slope, 3200 ft., 27 Feb. 1968, D. E. Breedlove 15,913 (holotype, GH; isotype, CAS).

Distribution. Mexico (Sinaloa).

The holotype of *Thelypodiopsis breedlovei* was initially annotated by Rollins as *Dryopetalon runcinatum* var. *laxiflorum* Rollins, and except for having crisped instead of laterally divided petals, the two taxa are almost indistinguishable in all other aspects except the fruit base. The fruits of *D. breedlovei* have a distinct gynophore, whereas those of *D. runcinatum* (including the varieties) are sessile.

2. *Dryopetalon byei* (Rollins) Al-Shehbaz, comb. nov. Basionym: *Thelypodiopsis byei* Rollins, Contr. Gray Herb. 212: 86. 1982. TYPE: Mexico. Chihuahua: Mun. Batopilas, Sierra Madre Occidental, along Arroyo Wimivo (Samachique) betw. Wimivo & Río Batopilas, on N side of Barranca de Batopilas, short-tree and thorn forest, 28 Feb. 1973, R. A. Bye 3433 (holotype, GH).

Distribution. Mexico (western Chihuahua).

This species is strikingly similar to *Dryopetalon breedlovei*, but it has lavender instead of white flowers, longer and broader petals (see couplet 8 in the key above) that are not crisped, purplish instead of yellowish anthers, and longer (4–6 cm) and sessile (vs. shorter [2–3 cm] and stipitate) fruits.

3. *Dryopetalon crenatum* (Brandegee) Rollins, Contr. Dudley Herb. 3: 202. 1941. Basionym: *Sisymbrium crenatum* Brandegee, Proc. Calif. Acad. Sci. 3: 111. 1891. *Cardamine crenata* (Brandegee) Brandegee, Zoe 5: 156. 1903. TYPE: Mexico. Lower [Baja] California: Sierra de la Laguna, 2 Jan. 1890, T. S. Brandegee 6 (holotype, UC; isotype, GH).

Iodanthus striatus M. E. Jones, Contr. W. Bot. 15: 126. 1929. TYPE: Mexico. Baja California: Todos Santos, 17 Feb. 1928, M. E. Jones 24189 (holotype, POM).

Dryopetalon crenatum var. *racemosum* Rollins, Contr. Dudley Herb. 3: 203. 1941. Syn. nov. TYPE: Mexico. Lower [Baja] California: Esperitor Santo Island, beach, 1 Apr. 1931, G. N. Collins, T. H. Kearney & J. H. Kempton 125 (holotype, GH).

Distribution. Mexico (Baja California Sur).

As in *Dryopetalon runcinatum* (see below), plants of *D. crenatum* exhibit considerable variation in the density of flowers along the racemes. The type of *D. crenatum* has laxly flowered racemes, whereas the type of variety *racemosum* has somewhat densely flowered racemes. In my opinion, these slight differences do not justify the division of the species into varieties.

4. *Dryopetalon membranifolium* Rollins, Contr. Gray Herb. 214: 21. 1984. TYPE: Mexico. Sinaloa: 51 km by rd. from Villa Union on rd. to Durango, 800 m, steep slopes with shrubby woods, just below oak zone, 11–12 Mar. 1970, W. R. Anderson & C. Anderson 6172 (holotype, GH).

Distribution. Mexico (Sinaloa).

This distinctive species is easily distinguished from the remainder of the genus by having emarginate petals without lateral lobes.

5. *Dryopetalon palmeri* (S. Watson) O. E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 10: 561. 1929. Basionym: *Cardamine palmeri* S. Watson, Proc. Amer. Acad. Arts 24: 38. 1889. *Sibara palmeri* (S. Watson) Greene, Pittonia 3: 12. 1896. TYPE: Mexico. Lower [Baja] California: Muleje, Gulf of California, near Saltwater, foothills, 25 Dec. 1887, E. Palmer 421 (holotype, GH).

Dryopetalon purpureum Rollins, Contr. Dudley Herb. 3: 204. 1941. Syn. nov. TYPE: Mexico. Lower [Baja] California: Magdalena Island, Mar. 1917, C. R. Orcutt 17 (holotype, GH).

Distribution. Mexico (Baja California Sur, western Sonora; Rollins, 1941).

The main differences given by Rollins (1941, 1993) to distinguish *Dryopetalon palmeri* from *D. purpureum* are the presence in the former of spatulate petals with a bifid to deeply divided terminal lobe (vs. broadly spatulate to obovate petals with an entire terminal

lobe) and lowermost fruiting pedicels ca. 1 (vs. 1.5–2) cm long. The lowermost pedicels in the type of *D. purpureum* are 1–1.5 cm long, in the type of *D. palmeri* are 0.9–1.3 cm, and in 11 additional collections annotated by Rollins as *D. palmeri* are 0.8–2 cm long. Furthermore, the degree of lobing along the petal margin is highly variable in the species, and the terminal lobe is often undivided and rarely bifid or deeply divided. As for petal shape and length of the claw, there is a continuous variation in both aspects and this variation does not correlate with the lobing of petals or with the length of fruiting pedicels. Therefore, I conclude that these two taxa are conspecific.

6. *Dryopetalon paysonii* (Rollins) Al-Shehbaz, comb. nov. Basionym: *Thelypodium paysonii* Rollins, Rhodora 59: 61. 1957. *Rollinsia paysonii* (Rollins) Al-Shehbaz, Taxon 31: 422. 1982. TYPE: Mexico. Coahuila: Cañon de Jara, E of Socorro, lower part of canyon near its mouth, ca. 30 km W of Cuatro Cienegas, 1–15 Feb. 1941, *Albert H. Schroeder* 12 (holotype, GH).

Distribution. Mexico (Coahuila, Durango; Al-Shehbaz, 1973).

7. *Dryopetalon runcinatum* A. Gray, Smithsonian Contr. Knowl. 5: 11. 1853. TYPE: Mexico. Chihuahua: s. loc., 1852, *C. Wright* 1314 (holotype, GH; isotype, MO).

Sisymbrium umbrosum B. L. Robinson, Bot. Gaz. 30: 60. 1900. *Coelophragmus umbrosus* (B. L. Robinson) O. E. Schulz, Pflanzenr. IV. 105(Heft 86): 158. 1924. TYPE: Mexico. Chihuahua: Puerta de St. Diego, shady places in rocks, 6500 ft., 12 Apr. 1891, *C. V. Hartman* 629 (holotype, GH).

Dryopetalon runcinatum var. *laxiflorum* Rollins, Contr. Dudley Herb. 3: 201. 1941. Syn. nov. TYPE: Mexico. Sinaloa: San Blas, 30 Jan. 1927, *M. E. Jones* 22842 (holotype, GH).

Distribution. Mexico (Chihuahua, Sinaloa, Sonora), United States (Arizona, New Mexico); see Rollins (1941).

Dryopetalon runcinatum is highly variable in the density of indumentum on the leaves and along the lower portions of the stem. In plants densely hirsute at the base, the sepals can be either glabrous (e.g., Ward 81-075, GH) or pubescent (e.g., Gentry 1992, GH), and in other collections there are but one or a few hairs on each sepal. This feature of indumentum does not correlate with the degree of lobing of petals or with the density of fruits in the infructescence. The species occupies diverse habitats ranging from open and sunny slopes or roadsides to shaded areas in canyons

and under protection of large boulders. When growing in the shade (e.g., Gentry 5379, GH), the plants have rather sparse indumentum near the base, are glabrous distally, and the fruiting racemes are rather lax versus somewhat densely flowered as in plants of sunny areas. Such plants are typical of what has been called variety *laxiflorum*, a taxon, in my opinion, that does not merit recognition.

8. *Dryopetalon viereckii* (O. E. Schulz) Al-Shehbaz, comb. nov. Basionym: *Arabis viereckii* O. E. Schulz, Notizbl. Bot. Cart. Berlin-Dahlem 11: 389. 1932. *Sibara viereckii* (O. E. Schulz) Rollins, Rhodora 43: 481. 1941. TYPE: Mexico. Nuevo León: Victoria, 27 Feb. 1930, *H. W. Vireck* 54 (holotype, B).

Arabis endlichii O. E. Schulz, Notizbl. Bot. Cart. Berlin-Dahlem 11: 390. 1932. *Sibara viereckii* var. *endlichii* (O. E. Schulz) Rollins, Rhodora 43: 479. 1941. TYPE: Mexico. Coahuila: Rancho de la Luz, Sierra & Hacienda de la Paila, 900 m, 1 Apr. 1905, *R. Endlich* 814 (lectotype, designated here, B).

Arabis runcinata S. Watson, Proc. Amer. Acad. Arts 17: 319. 1882, non *Arabis runcinata* Lamarek, Encycl. 1: 222. 1783. *Sibara runcinata* Rollins, Rhodora 43: 481. 1941. TYPE: Mexico. Near San Luis Potosí, shaded places, *J. G. Schaffner* 155 (holotype, GH).

Sibara runcinata var. *brachycarpa* Rollins, Contr. Gray Herb. 165: 138. 1947. TYPE: United States. Texas: La Salle Co., Cotulla, Mar. 1917, *E. J. Palmer* 11314 (holotype, RM).

Distribution. Mexico (Coahuila, Hidalgo, Nuevo León, Puebla, San Luis Potosí, Zacatecas), United States (southern Texas); see Rollins (1947).

Schulz (1932) cited two collections in his original description of *Arabis endlichii*. The more complete specimen with flowers and fruits is designated herein as the lectotype.

The species is highly variable in the division of cauline leaves, the size and development of leaf auricles, size of fruits (1.5–4.7 cm), length of fruiting pedicels (3–14 mm), and length of style (0.4–4 mm). Rollins (1947) divided it into two species and two varieties but later (1993) accepted a highly polymorphic species without infraspecific taxa. The species is somewhat anomalous in *Dryopetalon* for having latiseptate fruits to 3 mm wide (vs. terete or latiseptate but to 2 mm wide), auriculate (vs. non-auriculate) cauline leaves, and narrowly winged (vs. wingless) seeds. However, these differences are exhibited within many other genera of the family, and they are considered to be insignificant in the delimitation of this genus.

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